

ON SELECTIVE PRESSURES AND ENERGY ALLOCATION
IN POPULATIONS OF *RANUNCULUS REPENS* L.,
R. BULBOSUS L. AND *R. ACRIS* L.¹

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ABSTRACT

Selective pressures seen through patterns of mortality in plant populations seem to occur mostly in two fashions: (a) between germination and establishment for sexually reproducing species, and (b) at any moment, independently of age, during the adult life of vegetatively reproducing species. Studies on the mortality processes in three *Ranunculus* species in Welsh coastal grasslands showed that they are nonsynchronous for the three sympatric, closely related species. Studies on the distribution of biomass in vegetative and sexual structures showed a clear relation between rates of mortality and rates of individual growth, mortality being negligible at times of low individual growth. Comparisons of crude reproductive effort alone defined the vegetatively reproducing species (*R. repens*) as a "K-selected" species, while the exclusively or mostly sexually reproducing *R. bulbosus* and *R. acris* were shown to be "r-selected" species. However, when biomass expenditure on propagule production, whether by sexual or vegetative means is compared, all three species appeared to invest almost identical proportions of their biomass in structures aimed at maintaining population numbers at equilibrium. The possible significance of these patterns of energy expenditure in the three buttercups is discussed briefly.

There have recently been frequent references in the ecological literature to the imbalance between demographic information on animals and plants (Sarukhán & Harper, 1973; Harper & White, 1974, for example). Pleas for an increase on actuarial studies about plant populations have followed remarks on the lack of plant demographic studies, and indeed an answer is being given to those pleas. A clearly increasing number of direct actuarial studies (Hartshorn, 1972; Hawthorn, 1973; Hett & Loucks, 1971; Kays & Harper, 1974; Sarukhán & Harper, 1973; Sarukhán, 1974; Sarukhán & Gadgil, 1974; Sharitz, 1970; Symonides, 1974; Thomas & Dale, 1974; Werner, 1975); or the reinterpretation of data with potential actuarial information (Harper, 1967; Harper & White, 1974; Sagar & Mortimer, in press) have sprung from the initial thrust of the early pioneer works of Tamm (1956), Rabotnov (1950, 1956) and Sagar (1959), and are starting to form a body of information on plant ecology of a unique nature.

However, as soon as information coming from actuarial studies on plants began to be analyzed and interpreted in a common context with collateral information on various aspects of plant population biology, such as patterns of thinning in natural and sown populations, the plastic responses of plants to environmental stresses, mechanisms of density dependent mortality, etc., it became clear

¹ This study formed part of a Ph.D. research project at the School of Plant Biology, University College of North Wales, Bangor. I am deeply indebted to Prof. John L. Harper for his supervision of the research, his valuable ideas and suggestions, and the many technical facilities provided which made this part of the research possible. My thanks are due to Prof. I. M. Lucas for providing help at the College Farm, Henfaes and to the staff of the Pen-y-Fridd Experimental Station for their assistance. My studies were carried out with financial help from the Ministry of Overseas Development (G.B.) and the University of Mexico.

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that an uncritical adoption of methods and concepts of animal demography to the study of plant populations is not wise.

A discussion on some of the fundamental differences in the growth forms of higher plants and higher animals that have a profound bearing on their population behavior can be consulted in Harper & White (1974), so only a passing reference to this aspect will be made here.

Plant plasticity is perhaps the single most important factor determining the behavioral uniqueness of plant individuals and populations. Numerous examples have been cited concerning the enormous differences on the demographic contribution of individual plants of the same species under different environmental stresses [e.g., *Agrostemma githago* L. can vary the production of capsule numbers in a proportion of 6 to 1 due to increasing plant densities (Harper & Gajic, 1961)]. Even-aged populations develop extremely skewed distributions of individual size due to increased densities, especially when care has been taken in replenishing exhausted resources in the system (e.g., adding nutrients as density increases). Therefore, age may be a poor parameter for describing populational changes. For example, Werner (1975) has shown that *size* of plants of *Dipsacus fullonum* L. and *not age* is a much better element for making predictive statements concerning the death, survival and flowering of teasels.

There are numerous examples in forest literature showing a clearly marked lack of correlation between trunk diameter (d.b.h.) and chronological age, so interpretations of "population structure" based on the distribution of diameters often becomes confusing if not meaningless. However, data gathered on nearly 200 individuals of a pure stand of *Pinus hartwegii* Lindl. in Central Mexico have shown a remarkable positive correlation between age and d.b.h. (Sarukhán & Dirzo, in preparation).

MORTALITY PROCESSES

Although abundant data exists on mortality in plant populations, mostly man-managed populations, most of it is ancillary to demographic approaches and it is often difficult to interpret in terms of general patterns or processes of selective pressures.

One way of looking at selective pressures in plant populations is by the analysis of some of the available data on life-tables of plant species. Of the 3 types of survivorship curves first described by Deevey (1947), types I and III imply the existence of selective pressures concentrated on particular stages of the life histories of the organisms.

It is of particular interest that all the data available for species dependent on sexual reproduction show survivorship curves of Deevey type III, where selective pressures are stronger in the earlier (seedling) phases of the life cycle, while populations which maintain their numbers by vegetative reproduction show in most cases a clear exponential rate of mortality from the very first moments of the "birth" of the daughter plant (Sarukhán & Harper, 1973); this type of survivorship is often obtained when one observes populations of mature plants. It has been suggested elsewhere (Sarukhán & Harper, 1973) that the great mortality risks involved at the seedling stages in sexually reproducing species, may be more

the result of the genetic load of unfit genotypes than the problems for metabolic adjustment between the stages of the food dependent seedling and the self-sufficient established plant.

The safety of the vegetative reproduction as against the risky sexual reproduction in plants is illustrated with the probabilities of survival of seedlings and daughter plants of *Ranunculus repens* to the year next to their "birth." These probabilities are 0.12 for a seedling and 0.77 for a daughter plant. Another species, *R. acris* also showing both modes of reproduction has probability values of survival to one year of 0.12 for seedlings and of 0.71 for daughter plants.

Mortality processes in mature plants have been described in fair detail and a general principle on the way plant populations are thinned under pressures of density-dependent mortality seems to emerge from abundant data. This principle refers to the way individual plants of a population react plastically to environmental stresses so that a situation of a yield ceiling is achieved, a ceiling which is fixed by a slope very near to the $3/2$ power (Yoda et al., 1963; White & Harper, 1970; White, 1975) when log mean yield per plant is plotted against log density of survivors.

However, although a reasonably general description of mortality processes has been reached, the explanation of the mechanisms by which selective pressures act on natural populations still lies greatly in obscurity.

Analysis of the mortality processes in *Ranunculus repens* have shown that life expectancy of individuals, for example, decreased significantly with increasing density of the populations (Sarukhán & Harper, 1973). It was also clear that the highest mortality rates per week were obtained not in the unfavorable phases of the physical environment but were coincidental with the active growth of the plants.

Data from single species populations under experimental conditions also show clearly a higher mortality risk of individuals at the moment of maximum growth (Langer, 1956), and the same has been observed in natural populations of *Plantago rugelii* Decne. and *P. major* L. in Canada (Hawthorn, 1973).

Moreover, an analysis of the patterns of growth and mortality in *R. repens* shows rather clearly that the latter increases sharply when growth rates are highest and is negligible when growth is not occurring or is minimal.

Not only the detailed analysis of mortality patterns within a plant population can be revealing of the source and strength of selective pressures, but also the general mode in which these pressures incide on the life cycle of plants.

A comparison of the occurrence of mortality pressures among the three closely related sympatric species *Ranunculus repens*, *R. bulbosus*, and *R. acris* has shown striking differences in the manner in which mortality acts in regard to time of the year and stages in life cycles.

The major periods of mortality in mature populations of the three species of *Ranunculus* occurred during spring and early summer but were not synchronous. The process of mortality started earliest in *R. bulbosus*; it was followed by *R. acris* and finally by *R. repens*. A prereproductive peak of mortality occurred in all the species. It was earlier in *R. bulbosus* than in *R. acris*, *R. repens* being

clearly the latest. A postreproductive peak of mortality also was obvious, and was more conspicuous than the prereproductive peak in *R. repens* and *R. acris*.

A conspicuous trough in mortality occurred in the three species coincidental to the time at which maximum flowering was taking place.

The seasonal pattern of mortality of the newly recruited population showed even greater differences between the 3 species: (a) Mortality of newly recruited vegetative propagules in *R. repens* follows closely that of the mature individuals while populations of newly emerged seedlings of *R. bulbosus* and *R. acris* constituted a distinct period of mortality in the population. (b) Times of occurrence of seedling mortality vary from early to late spring for *R. acris* and *R. repens*, respectively, and to late autumn for *R. bulbosus*.

The high risk of death involved in maintaining or replacing population numbers by seeds, reflect the experimental nature of the sexual propagules, and it is here where selection against unfit genotypes must occur.

The ramets or vegetative propagules represent tested genotypes which can expand clonally or contract depending on the current year's environmental conditions, but they always seem to be represented in the populations and ready to expand when conditions are amenable for a given genotype.

Direct evidence on the selective nature of mortality forces is nonexistent in the few available plant demographic studies since genotypes have not been studied and their performance or fitness tested. However, indirect evidence suggests that mortality acts on certain individuals of the population, particularly weak, nonaggressive plants, and selective pressures like competition or grazing certainly do affect the amount of progeny left by different genets in a population.

ENERGY ALLOCATION

The characteristics of living organisms cannot be defined in space alone—a herbarium specimen of a buttercup defines its form only at one point in time. The individual plant or animal has a life cycle with a temporal pattern of growth and development that is repeated over the generations. This recurring cycle is a fundamental property of living as opposed to purely physical systems and is the element which confers much of the interest in demographic studies.

In the course of its life cycle an organism accumulates materials and energy available in its environment and disposes of them in the production of different organs. Cody (1966) and MacArthur & Wilson (1967) have pointed out that natural selection will operate on the form in which the resources are allocated by the organism in such a way as to maximize its contribution to future generations. Selection acts on an "adaptive surface" in which what is "spent" on one structure cannot be spent on another. Morphology of organisms can therefore be thought of as the selective compromise of resource allocation to different organs which results in a successful strategy for a species, and in comparing species it is highly relevant to enquire how they differ in such allocation and strategy. Allocation of energy to reproduction as opposed to structures which may confer aggressiveness (height, extensive roots, etc.) or resistance to predators (spines, toxins, etc.) is often of prime interest.

Theoretical ecologists have recently laid much stress on the concept of "r" and "K" strategies, recognizing that the selective forces acting on species that spend most of their life as colonizers are different from those that suffer density stress in stable communities. Colonizing species ("r" strategists) are envisaged as the result of selection for high fecundity; such species allocate large proportions of their available resources to reproduction and little to structures that allow them to become better established in their community or to avoid predation; therefore, high fecundity is often linked to low aggressiveness. In contrast, species of closer or more stable habitats ("K" strategists) may have improved their long term survival by devoting a great proportion of their resources to structures which confer advantages to individuals in the struggle for existence, although at the cost of reduced fecundity. The study by Gadgil & Solbrig (1972) on "r" and "K" selection in plants is an outstanding example of this approach.

Ogden (1968) has compared a few plant species with respect to the proportion of their annual assimilation that is devoted to seed production and showed that, in general, annuals had high values (30–40%) and perennials, particularly those reproducing vegetatively, had low values (5–10%).

This "reproductive effort" of the species should ideally be determined by knowing the proportion of the total energy of the plant as starting capital (i.e., as an embryo) plus its gross assimilation that is invested in propagules (Harper & Ogden, 1970); but because there are obvious technical difficulties in assessing gross assimilation, approximate but more practical forms have been used in the estimation of reproductive efficiency. The "harvest index" of crop plants (e.g., Donald, 1962; Stern & Beech, 1965) estimates the reproductive effort of species as the proportion of the total weight or biomass of plants at maturity that is allocated to propagules. Harper & Ogden (1970) have used the calorific energy allocated to reproduction for the description of the strategic distribution of the resources of a plant.

The data on plant growth and dry matter allocation which follows was obtained to complete a comparative demographic study of three *Ranunculus* species. It was intended to provide the necessary information to understand inter- and intraspecific interactions of the three species, as well as to throw more light on the interpretation of the actuarial data gathered for the three species.

Plants of *Ranunculus repens*, *R. bulbosus*, and *R. acris* growing under natural conditions in the University College of North Wales experimental field at Aber, Gwynedd, were used for the study during the growing season of 1969. The biology of the species and the characteristics of the site have been dealt with elsewhere (Harper, 1957; Sarukhán & Harper, 1973).

Two contrasting sites of collection for each species were selected, based on the degree of grazing of the site. Thus, for each species site I represents the more intensely and site II the more lightly grazed condition. Twenty mature plants of each species were sampled at random within each site at the following dates in 1969: 20 April, 17 May, 29 May, 16 June, 23 June, 30 June, 6 July, 16 July, and 1 August. This period covered most of the growing cycle of the three species.

Adequate extraction of root material from the soil presents a major obstacle to studies of productivity and dry-matter allocation in plants. Bearing in mind

that it is an impossible task to extract whole root systems from the soil the following procedure was adopted to obtain a common basis for comparison of the energy allocated to roots in the three species of buttercups. A special metallic cylinder was placed carefully around a buttercup plant and a soil core of constant volume (5.3 cm in diameter, 9 cm deep = 200 ml) was obtained. The metallic sampler had sharp edges to facilitate cutting through the superficial root mat and to reduce compaction of the soil when sampling. Two metallic wings 9 cm from the edge of the sampler ensured that samples of soil exactly 9 cm deep were obtained.

Once collected, the soil cores containing the plants were placed separately in labelled polythene bags and transported to the laboratory. The cores were soaked in water in separate containers and then placed under a gentle jet of water to remove the soil particles; the plant material was sorted by hand and the maximum possible amount of roots recovered; this operation was carried out over a very fine sieve that retained loose roots. Although it was possible to train the eye to distinguish the roots of the three species of buttercups from those of other species present, a considerable proportion of the very fine rootlets that became loose could not be identified with certainty and therefore was not included with the rest of the plant material. Each plant was partitioned into several components:

R. repens: 1. Rosette leaves with petioles. 2. Stolon leaves with petioles. 3. Roots of the main rosette. 4. Stolons (sometimes including rootlets in the nodes). 5. Stems (the remainder of the vegetative aerial part of the plant after having removed petioles, roots and stolons). 6. Flowers. 7. Fruits (achenes and the fruiting head).

R. bulbosus: 1, 3, 5, 6, 7, 8. Corm.

R. acris: 1, 3, 5, 6, 7. Stems in *R. bulbosus* and *R. acris* included floral stems.

The data presented refers to the standing crop or biomass of the plants at the moment of harvest. As plants of the three species, particularly *R. repens* and *R. bulbosus* undergo more or less complete physiological renewal every year, it is probable that their biomass in the initial phases of growth did not differ greatly from their net dry matter production. However, some dry matter may have been lost through grazing and tissue decay in the later samplings. Ogden (1968, 1970), for example, estimated that in high density stands of *Tussilago farfara* L., maximum biomass of the plants represented only from 55–60% of their total net dry matter production.

BIOMASS PRODUCTION WITH TIME

Plants of the three species started the year's growth with a very similar initial weight (Figs. 1–3) and showed different peaks of maximum dry matter production. Plants collected in Site II (with light grazing) appeared in general to be more productive than those in the more intensely grazed zones (Site I). This was particularly true for *R. repens* which in the lightly grazed zone showed a remarkable exponential growth between April and the middle of June, reaching a peak at the end of this month and then decreasing sharply towards July.

Plants of *R. bulbosus* in the intensely grazed sites showed two clear peaks of

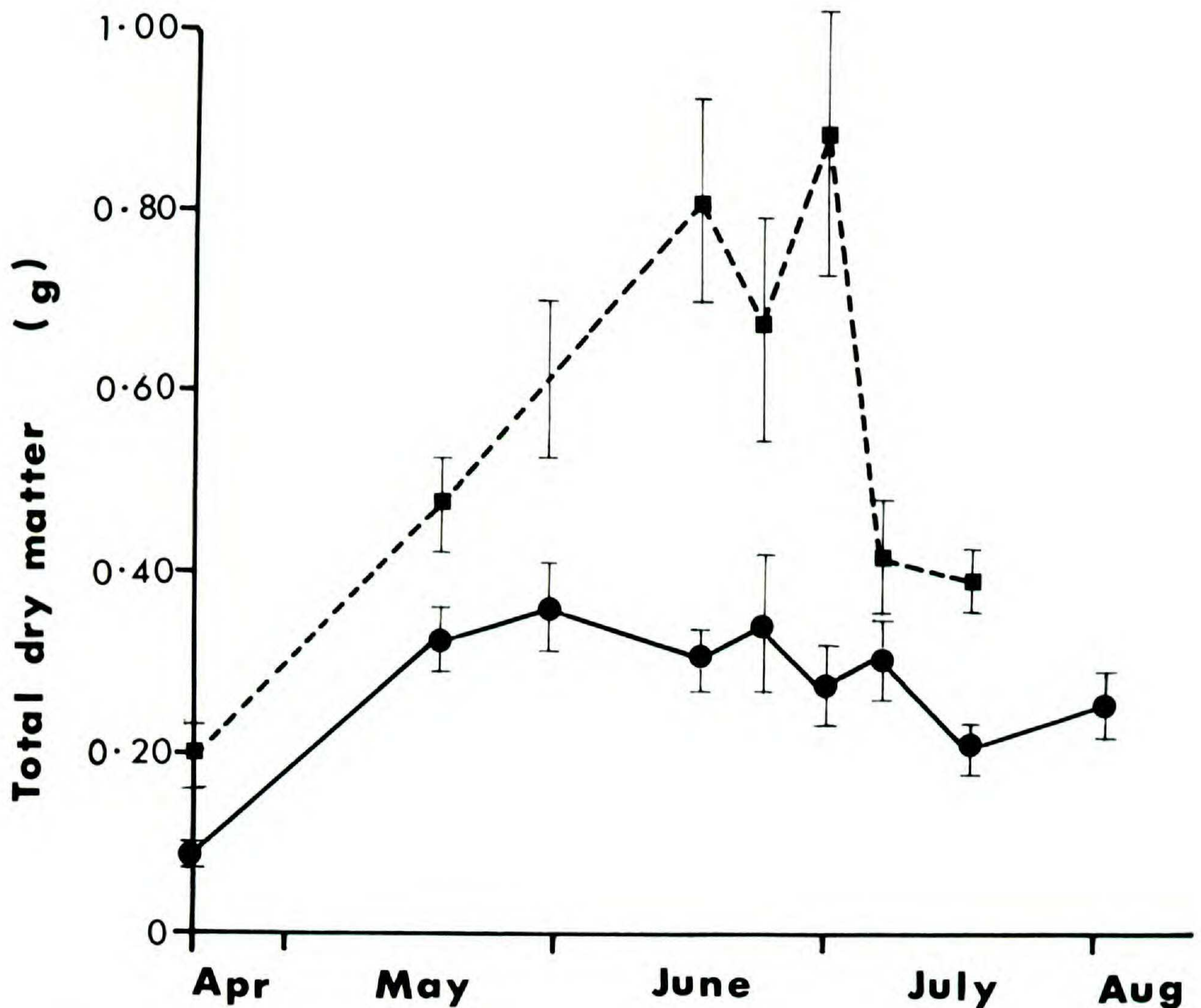


FIGURE 1. Total dry matter produced by plants of *Ranunculus repens* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

biomass production; the peak occurred earlier in the lightly grazed than in the more intensely grazed sites.

Plants of *R. acris* in the intensely grazed sites also showed two peaks of biomass production in early July and early August and attained the highest weights recorded for any of the three species.

In order to obtain an idea of the "crop" growth rates presented by the three species, the log. of the total dry weight has been plotted in Fig. 4 for the average values of all plants of each species collected in both sites.

Three phases can be distinguished in the curves. The first from April to the end of May or mid-June represents the rapid growth of the winter rosettes at the time of production of new leaves and roots. The second phase, when the growth rate is nearly zero, coincides in *R. repens* with the initiation of stolon growth and elongation and in *R. bulbosus* and *R. acris* with the production of the floral stem carrying floral buds. At this stage, a number of old leaves may have decayed and were probably not collected and may account partly for the reduction in total biomass; the third phase, a negative growth rate, is clearer in *R. repens* and *R. bulbosus*. Many plants of *R. repens* that produce stolons lose all

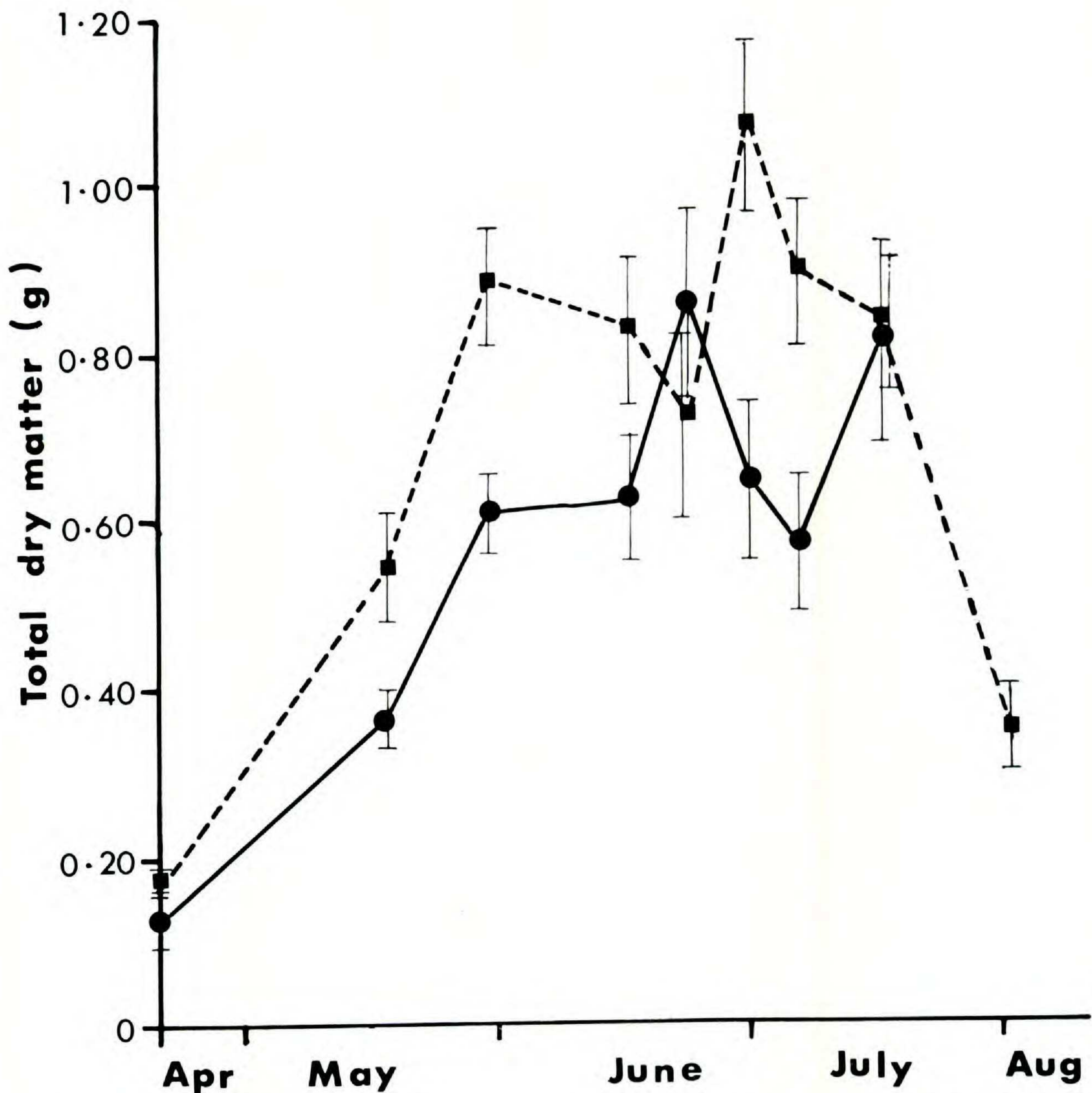


FIGURE 2. Total dry matter produced by plants of *Ranunculus bulbosus* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

their leaves at this period and eventually die. All the aerial structures of *R. bulbosus* have withered and disappeared by the end of July, when the biomass of these plants is totally represented by the buried corm. This third phase of negative growth rate was not observed for plants of *R. acris* in the study period.

Figures 5–7 show the growth of the different parts of the plants with time. In all the species, the initial period of growth is contributed chiefly by leaves and roots as the plants change from the winter form to the spring form of the rosette. Subsequent growth in *R. repens* is mainly contributed by the production of stolons with their leaves and an increase in the root system that supports the early phases of stolon production. In *R. bulbosus* the corm and the floral stems represented a great proportion of the total dry matter produced by plants from the end of May onwards. There was consistently only a very small growth of the root system.

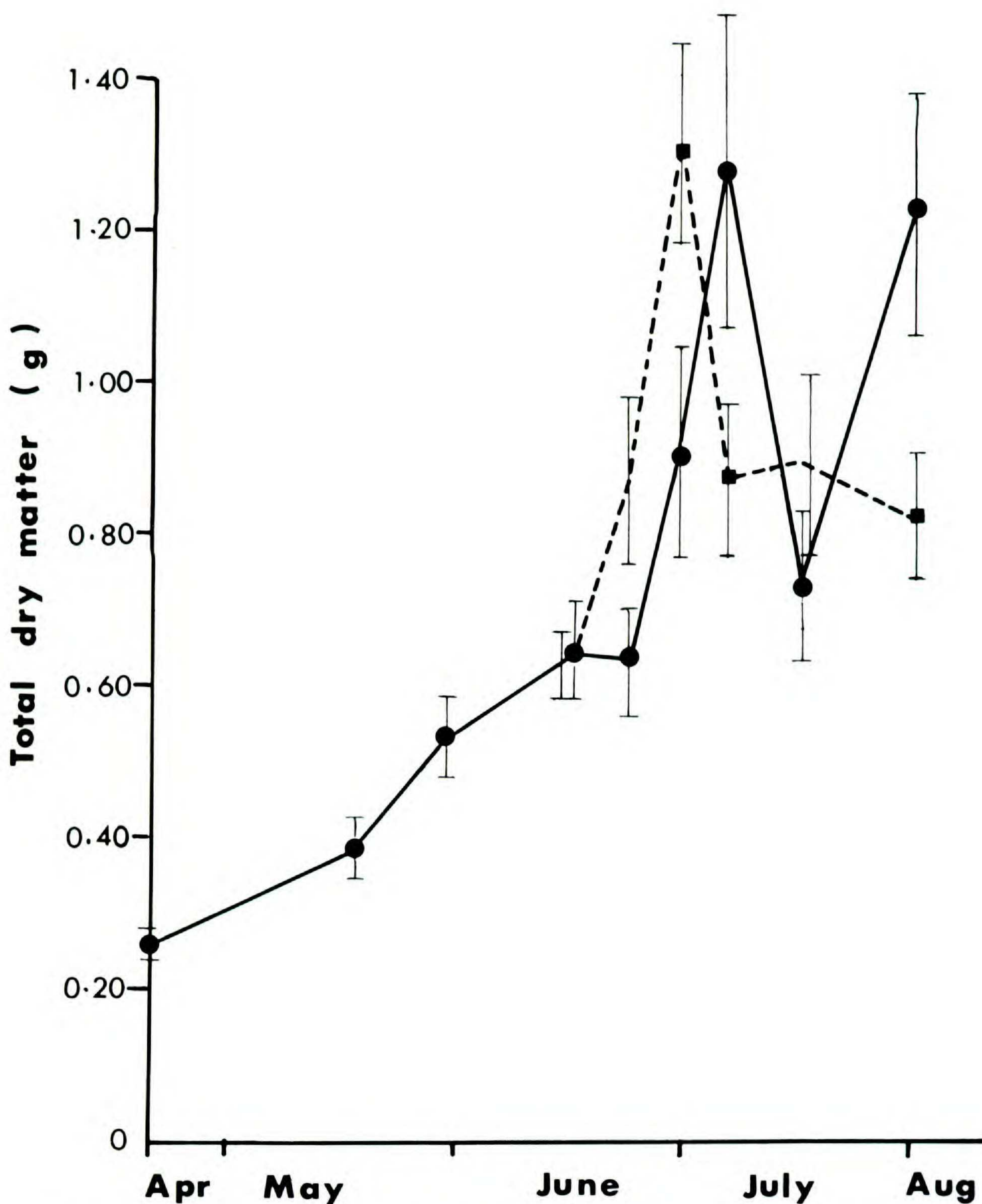


FIGURE 3. Total dry matter produced by plants of *Ranunculus acris* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

The root system in *R. acris* appeared to be better developed than in the other two species; it contributed a substantial amount of the total biomass. The relative contribution of leaves to the total biomass declined at the end of May when the floral stems together with flowers and achenes become the predominant parts of the total biomass. The similarity between the total weight of flowers plus achenes in plants of *R. bulbosus* and *R. acris* is very striking.

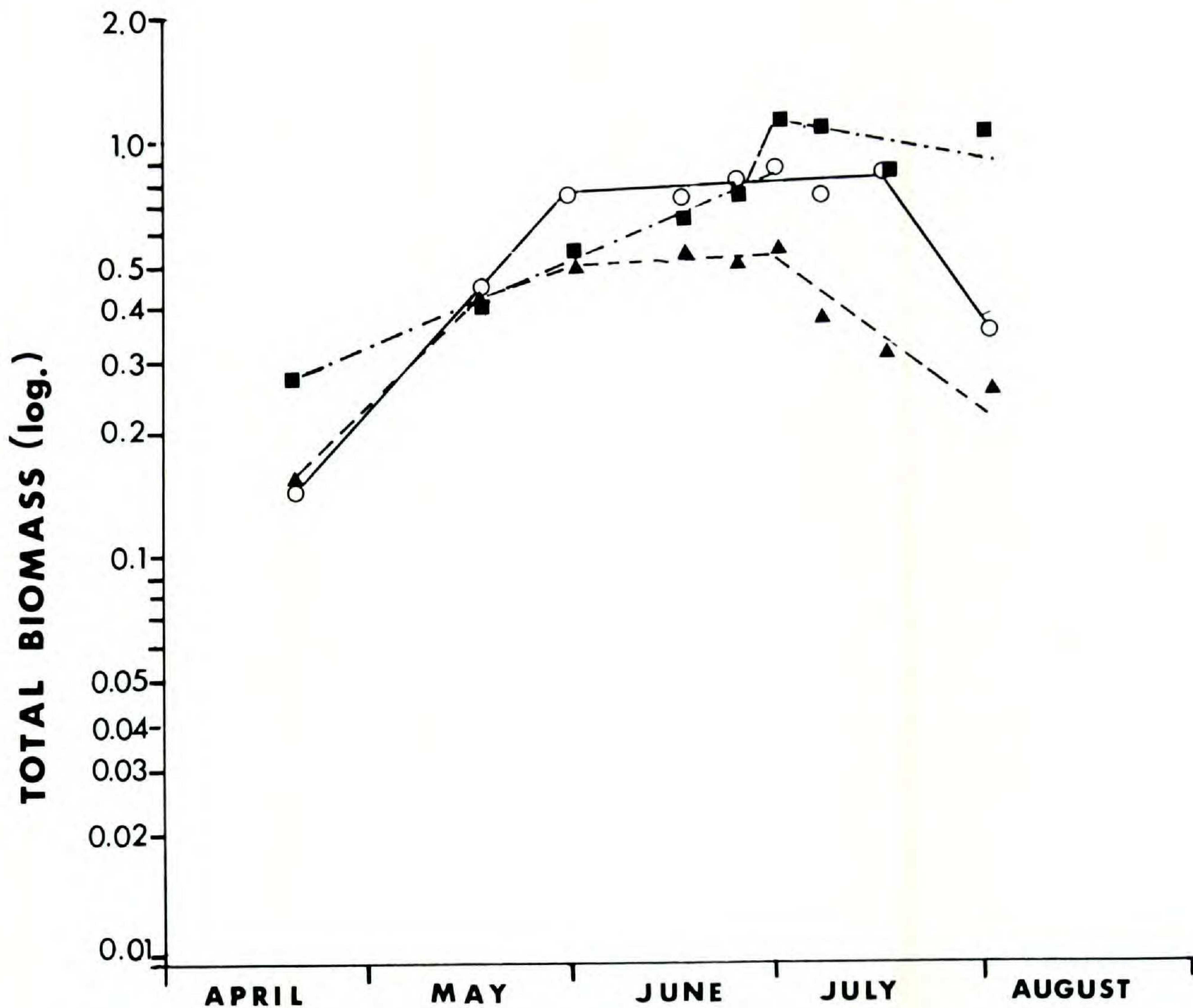


FIGURE 4. Growth rates of plants of *Ranunculus repens* (solid triangles), *R. bulbosus* (open circles), and *R. acris* (solid squares).

THE DISTRIBUTION OF BIOMASS

The patterns of distribution of biomass in plants of the three species of *Ranunculus* are shown in Figs. 8–10. The percentages are derived from averages of 40 plants collected for each species at each date. One of the two more striking points is the difference in dry matter allocated to flowers and seed in *R. repens*—the vegetative reproducer—and *R. bulbosus* and *R. acris*—the seed reproducers. The second point is the similarity of the dry matter allocated to the whole reproductive system of *R. repens* (stolons, stolon leaves, flowers and seed) to the total dry matter allocated to reproduction-related structures in *R. bulbosus* and *R. acris* (floral stems plus flowers and seeds). The constantly low contribution of roots to the total biomass of *R. bulbosus* contrasts with the contribution of roots in the other two species. The high proportion of corm and low proportion of roots in *R. bulbosus* suggest that the summer dormancy of this species may permit it to avoid water stress. It may also be that the roots of *R. repens* and *R. acris* play some of the food storage role that the corm plays in *R. bulbosus*.

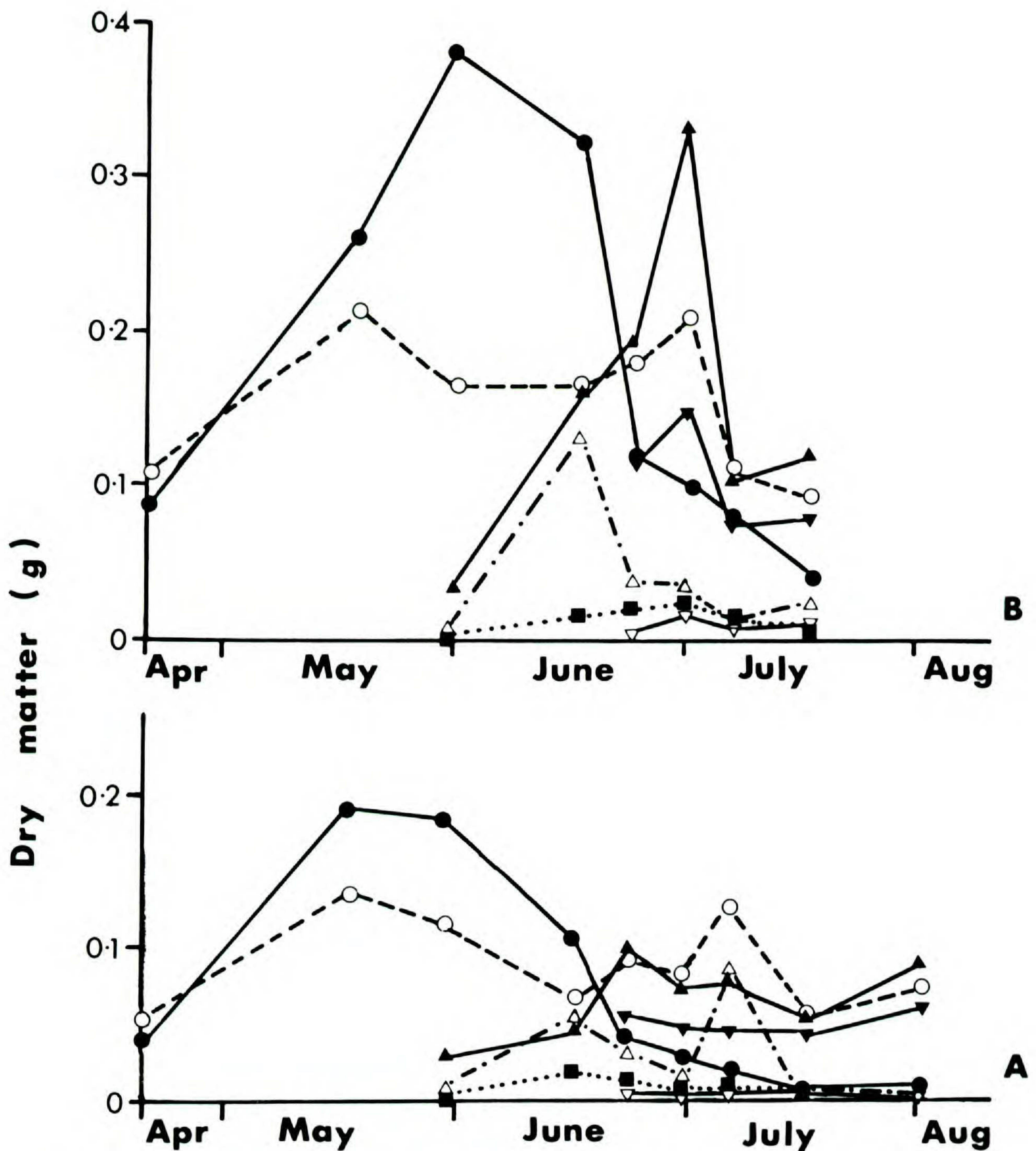


FIGURE 5. Total dry matter produced by the different organs of plants of *Ranunculus repens* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in an intensely grazed site (A) and a lightly grazed site (B). Leaves (solid circles), roots (open circles), stolon leaves (solid triangles pointing downward), stolons (solid triangles, pointing upward), stems (open triangles, dotted lines), flowers (solid squares), and achenes (open triangles, solid lines).

REPRODUCTIVE EFFORT

The proportions of dry matter allocated by each of the three species to: (a) the production of achenes, (b) the production of ancillary structures to sexual reproduction (floral parts, floral stems), and (c) to vegetative propagules (stolons, stolon leaves) are shown in Table 1. It is difficult to assign the stolon leaves definitely as a cost to the parent plant; they may initially be "placental" demand-

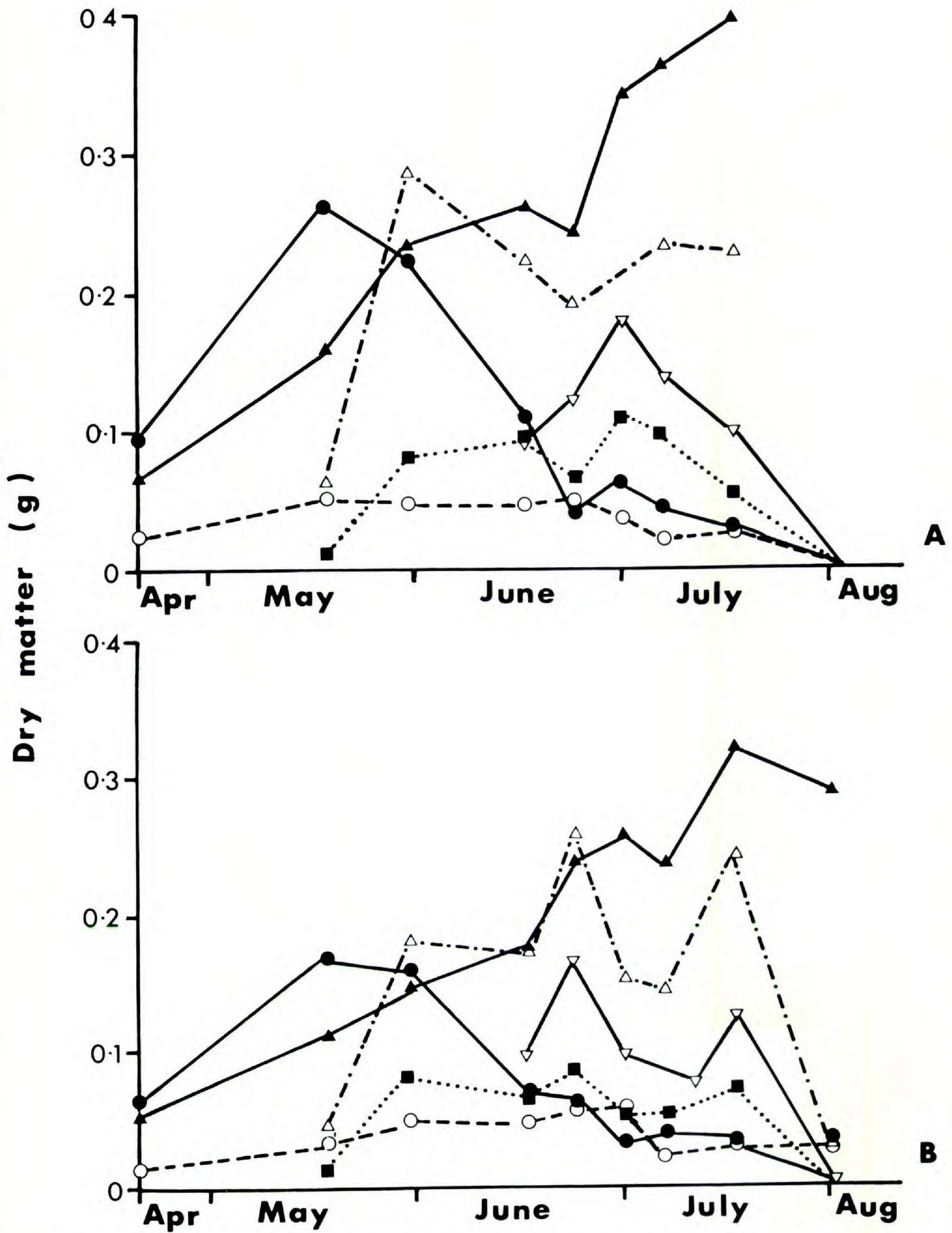


FIGURE 6. Total dry matter produced by the different organs of plants of *Ranunculus bulbosus* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in an intensely grazed site (A) and a lightly grazed site (B). Leaves (solid circles), roots (open circles), corn (solid triangles), stems (open triangles, dotted lines), flowers (solid squares), and achenes (open triangles, solid lines).

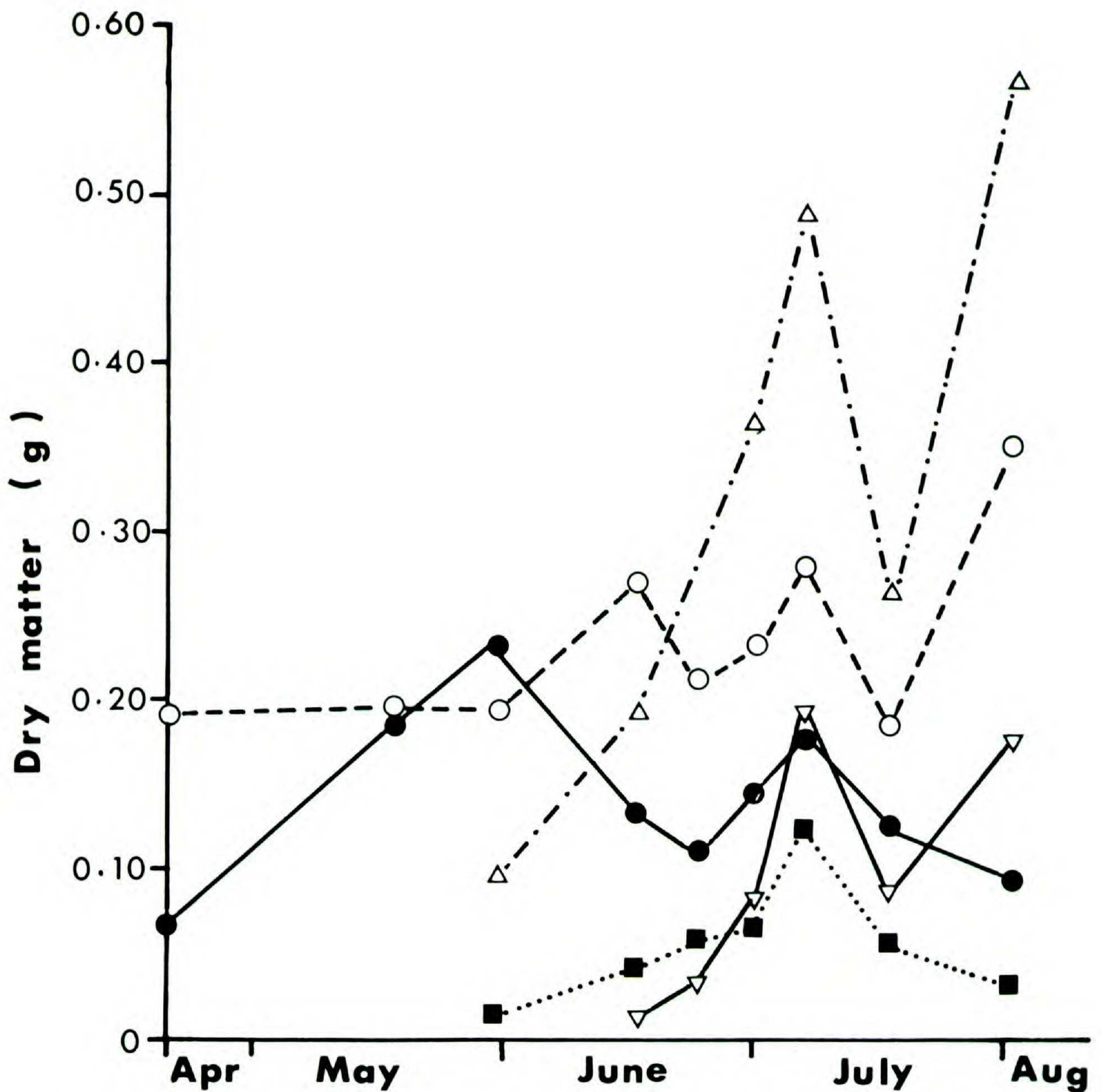


FIGURE 7. Total dry matter produced by the different organs of plants of *Ranunculus acris* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in a lightly grazed site. Leaves (solid circles), roots (open circles), stems (open triangles, dotted line), flowers (solid squares), and achenes (open triangles, solid lines).

ing structures but obviously at some stage acquire a positive assimilatory role. If the proportion of dry matter allocated to achenes only (weight of achenes/total dry weight) as a crude reproductive effort is considered, *R. bulbosus* and *R. acris* appear to have high reproductive efficiency (ca. 15 and 11%, respectively) and *R. repens* has a low reproductive efficiency (between 1 and 5%). However, if dry matter allocated to all propagules (both seed and vegetative) is considered, the situation is different. The three species appear to have "spent" almost the same proportion of their biomass to reproductive ends (either sexual or vegetative); the sum of the allocation to achenes plus ancillary structures plus vegetative reproduction in *R. repens* between June 23 and July 16 varied from 48–58%; the comparable figure in *R. bulbosus* in the same period was 49–52%, and for

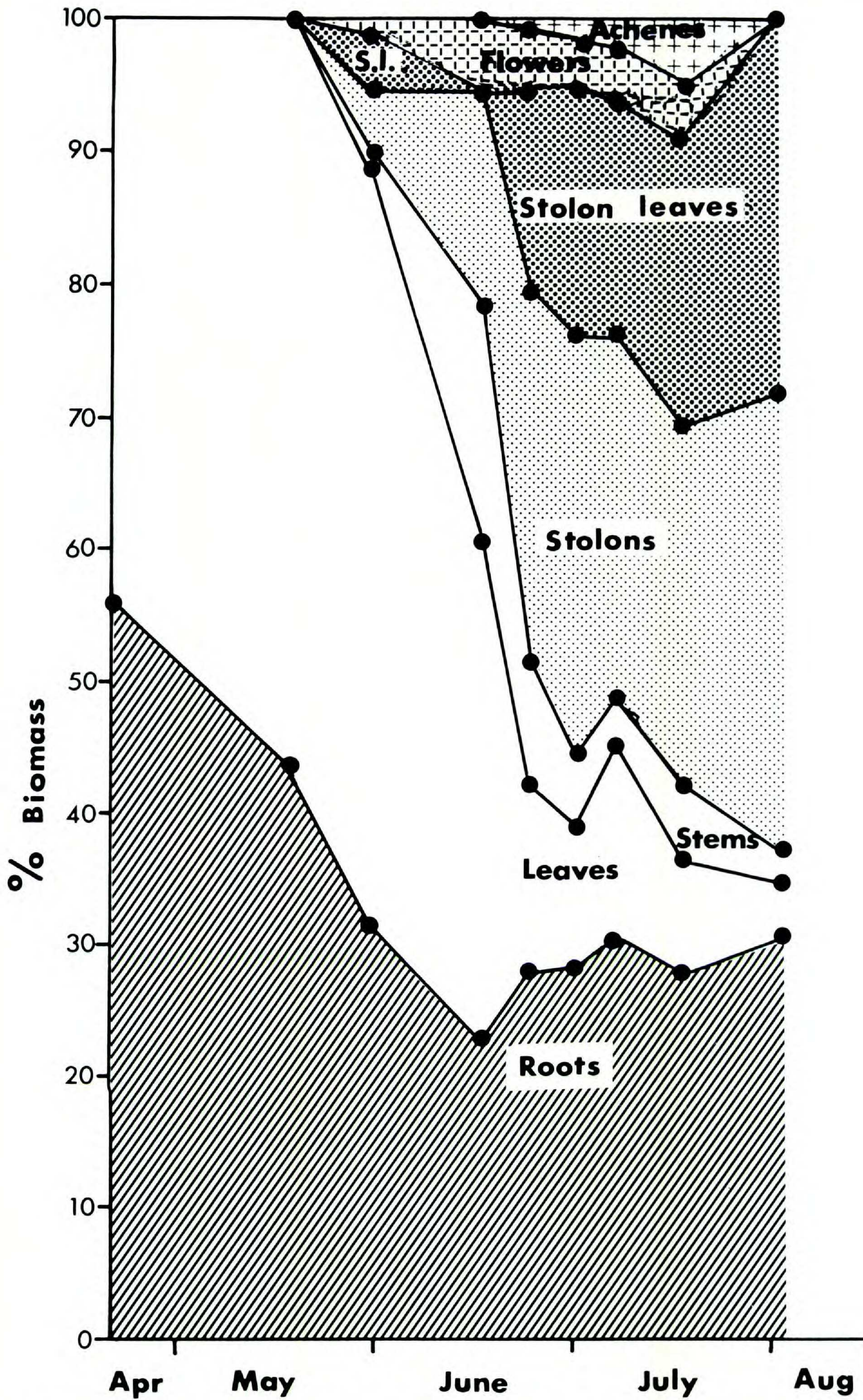


FIGURE 8. Distribution of the total biomass of plants of *Ranunculus repens* to their different organs. Data are averages of 40 plants.

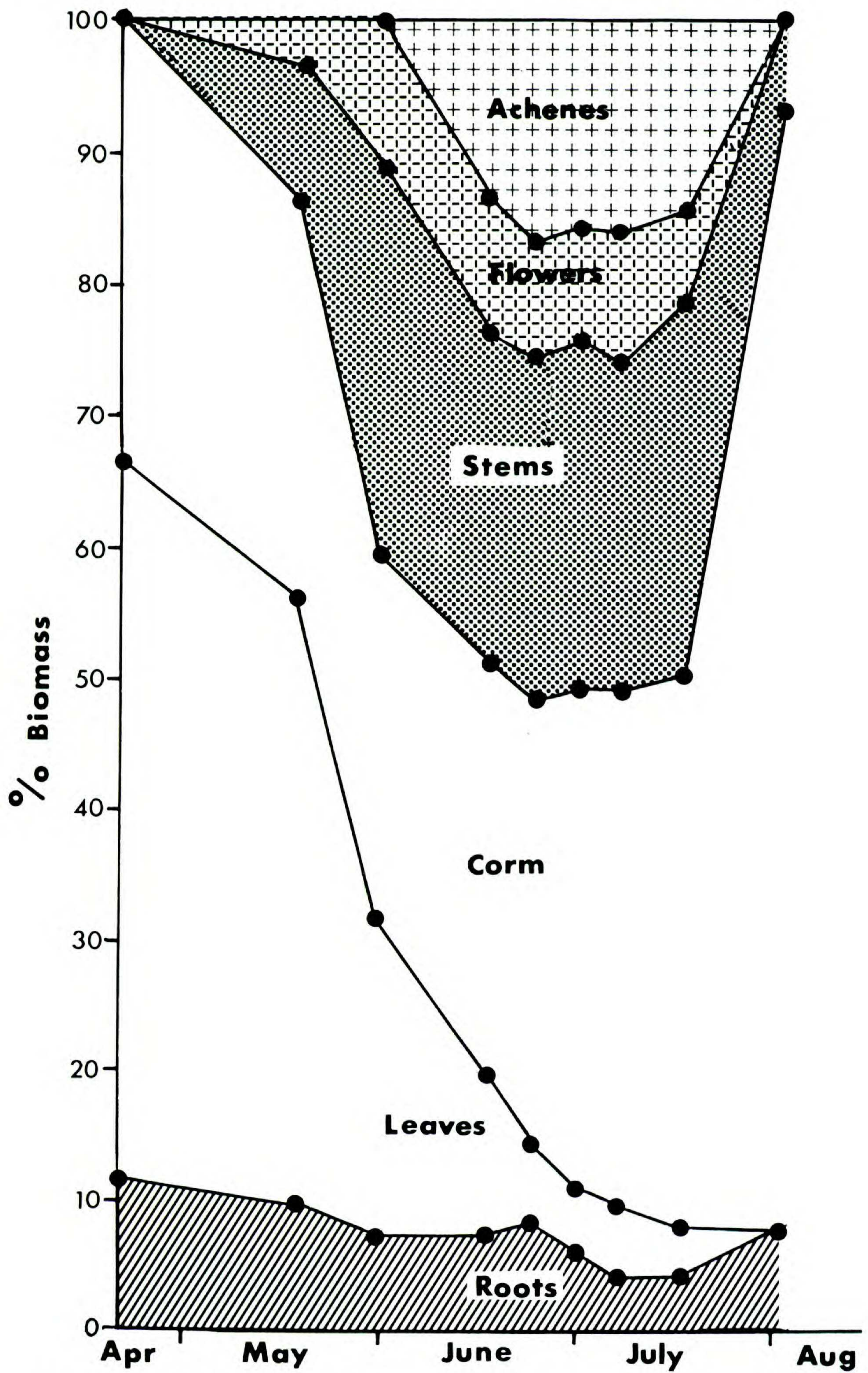


FIGURE 9. Distribution of the total biomass produced by plants of *Ranunculus bulbosus* to their different organs. Data are averages of 40 plants.

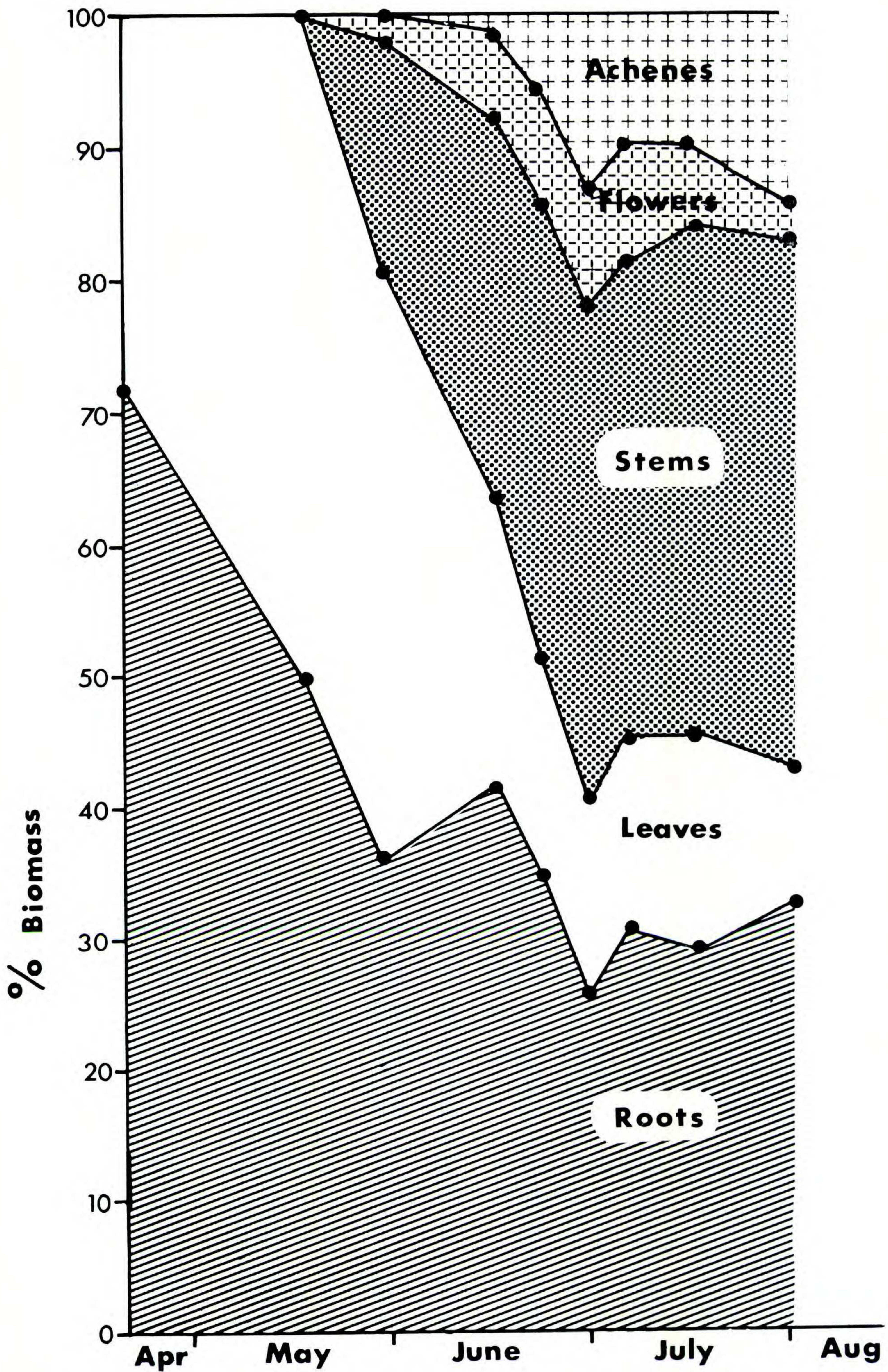


FIGURE 10. Distribution of the total biomass produced by plants of *Ranunculus acris* to their different organs. Data are averages of 20 plants.

TABLE 1. Crude reproductive effort (weight of achenes/total biomass \times 100) and % of total biomass allocated to flowers and floral stems and to vegetative reproduction by plants of *Ranunculus repens*, *R. bulbosus*, and *R. acris*. Values for each species are averages of 40 plants.

Date	Achenes only (crude rep. effort)	Flowers and floral stems	Vegetative reproduction	Total reproduction
<i>R. repens</i>				
29/5	0	2.0	9.4	11.4
16/6	0	4.6	16.9	21.5
23/6	0.8	4.7	43.0	48.5
30/6	1.6	3.4	50.3	55.3
6/7	2.1	4.0	45.1	51.2
16/7	4.8	4.3	48.9	58.0
1/8	0	0	62.9	62.9
<i>R. bulbosus</i>				
17/5	0	13.8	—	13.8
29/5	0	41.6	—	41.6
16/6	13.3	35.4	—	48.7
23/6	16.8	34.9	—	51.7
30/6	15.7	34.0	—	49.7
6/7	15.9	34.9	—	50.8
16/7	14.0	34.9	—	48.9
1/8	0	0	—	0
<i>R. acris</i>				
29/5	0	19.2	—	19.2
16/6	1.5	34.7	—	36.2
23/6	5.7	42.7	—	48.4
30/6	13.7	46.2	—	59.9
6/7	9.7	44.8	—	54.5
16/7	9.7	44.3	—	54.0
1/8	14.2	42.7	—	56.9

R. acris it was from 48–60%. It might then be argued that vegetative reproduction in *R. repens* is obtained at the expense of reproduction by seed.

The data on total reproductive effort of the three buttercups, but particularly that of *R. repens*, are in close agreement with information recently obtained for *Hieracium floribundum*, Wimm. & Grab., a perennial, rosette-forming, vegetatively-reproducing species. Thomas & Dale (1974) report for this species in old pastures in Canada a total reproductive effort (inflorescences and stolons) of between 64 and 74% (depending on density stresses) of the dry matter of the plant, excluding the root system, which causes an overestimation of the reproductive effort.

The crude reproductive efficiencies obtained for *R. bulbosus* and *R. acris* (Table 1) are very close to those obtained by Struik (1965) for perennial species for woodland and sand barrens in Wisconsin (12 and 15%, respectively), but are considerably lower than the values summarized by Ogden (1968) for weedy cultivated annuals (20–40%). The dry matter produced by reproductive plants of *R. acris* in upland meadows in the Moscow region (Rabotnov & Saurina, 1971) was considerably less (0.5 g) than the plants measured in the present study at College Farm, Aber (0.6–1.3 g).

The following conclusions on dry matter allocation in the three buttercups can be drawn: (a) the rate of growth of *R. repens* and *R. bulbosus* was greater but their growing cycle was shorter than that of *R. acris*; plants of *R. bulbosus* showed the most precocious spring growth; (b) the peaks of growth in the three species occur at different times in coincidence with differences of times at which maximum selection pressures occur; (c) grazing reduced the biomass of *R. repens* but had little effect on the other species; this probably reflects the different palatabilities of the three species; (d) an estimate of reproductive effort must include all the energy allocated by plants to reproduction, whether vegetative or by seed. The vegetative reproducer (*R. repens*) appeared in this respect to have about the same reproductive effort as the seed reproducers (*R. bulbosus* and *R. acris*). Even these two species fall very short of the reproductive efficiency of annuals (Ogden, 1968) and are of the same order as Ogden's values for *Tus-silago farfara*. Perhaps the very possession and maintenance of a perennial system involves budgetary costs that are offset by a lower reproductive effort.

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